



# Patterns and occurrence of diel vertical migration of zooplankton biomass in the Mid-Atlantic Bight described by an acoustic Doppler current profiler

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Received 10 November 1994, revised 6 January 1997; accepted 14 May 1997

## Abstract

The seasonal occurrence, timing, and pattern of diel vertical migration of acoustically estimated zooplankton biomass at the edge of the continental shelf off the eastern United States is described based on the SEEP II (Shelf Edge Exchange Processes in the Southern Middle Atlantic Bight) data set obtained between February 1988 and May 1989. Zooplankton biomass was estimated using a bottom-moored, upward-looking 300 kHz acoustic Doppler current profiler deployed at the 90 m isobath. Vertical distributions of biomass were represented by the median depths of the acoustically estimated biomass which had been normalized relative to the maximum and minimum depths for each day and time standardized such that sunrise and sunset occurred at 0600 and 1800, respectively. Periods of diel vertical migration during the 15 month record were identified by determining daily least-squares fits of hourly vertical velocities to an ideal curve of migrating biomass velocities such that maximum upwards and downwards velocities of zooplankton biomass coincided with sunset and sunrise, respectively. Diel vertical migration occurred for 35, 15, and 20% of the days ( $p < 0.05$ ) during each of the spring, summer, and fall/winter mooring deployments, respectively. The occurrence of diel vertical migration at the site appeared to be affected primarily by changes in the community composition of the zooplankton which was strongly influenced by the advection of different water types and associated zooplankton communities over the site. Little correlation was observed between the occurrence or magnitude of vertical migration and environmental parameters such as

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chlorophyll *a* concentration and temperature. Daily vertical migrations were timed to the diel light cycle. © 1998 Elsevier Science Ltd. All rights reserved

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## 1. Introduction

The diel vertical migration of zooplankton, both classic downward migration and 'reverse' upward migration during night, is a widespread phenomenon in aquatic systems and is characteristic of many zooplankton species and of much of the zooplankton biomass in some areas (e.g. Cushing, 1951; Raymont, 1963; Hutchinson, 1967; Longhurst, 1976; Ohman et al., 1983; Forward, 1988; Neill, 1990). The distribution of biomass with depth through time follows a sinusoidal curve during diel vertical migration (DVM) (Pearre, 1979; Roe et al., 1984). A particularly intriguing aspect of the migration pattern is the observation of 'midnight sinking', an increase in the depth of the population's abundance maximum during the middle of the dark period (see Raymont, 1963; Hutchinson, 1967; Forward, 1988).

Although much speculation and study have been expended on the topic, the underlying cues and causal mechanisms driving these migrations are still debated. Factors influencing diel vertical migration can be grouped in two categories: control or proximate mechanisms, such as environmental cues (light, temperature, food, chemical), and ultimate mechanisms, such as adaptive significance and selective pressures (avoidance of predation, metabolic advantage) (e.g. Enright, 1977; Forward, 1988; Haney, 1988). Field studies and experimental manipulations in freshwater and semi-enclosed marine systems have demonstrated that avoidance of predation, cued by the presence of predators or their chemical scent alone, is associated frequently with diel vertical migration (e.g. Zaret and Suffern, 1976; Ohman et al., 1983; Gliwicz, 1986; Neill, 1990; Bollens and Frost, 1991; Bollens et al., 1994). The distribution and concentration of food (e.g. Bohrer, 1980; Boyd et al., 1980; Huntley and Brooks, 1982; Dagg, 1985; Johnson and Jakobsen, 1987; Gliwicz and Pijanowska, 1988; Harris, 1988) may also influence the inception of diel vertical migration. Light is usually regarded as the primary stimulus for diel vertical migration and is considered to regulate the timing of migrations (e.g. Russell, 1927; Ringelberg, 1964, 1991, 1993; Hutchinson, 1967; Stearns and Forward, 1984, 1988; Forward, 1988; Haney, 1993). It is increasingly clear that diel vertical migration in aquatic systems has evolved in response to a combination of pressures or factors, especially food availability and the avoidance of predation, and may be cued by several environmental characteristics (e.g. Johnson and Jakobsen, 1987; Pijanowska and Davidowicz, 1987; Gabriel and Thomas, 1988; Lampert, 1989, 1993; Dini and Carpenter, 1991).

Most previous studies of vertical migration in the open ocean were conducted using day-night pairs of net tows (e.g. Roe, 1972; Roe et al., 1984; Angel, 1989) or pump samples (e.g. Checkley et al., 1992) to determine the vertical distribution of zooplankton. The time required to conduct such sampling constrained these studies. Often, they lacked detailed information on spatial and temporal variability, on replicability of observed migration patterns, and on seasonal changes in migration patterns.

Recently, the acoustic Doppler current profiler (ADCP) has been used to describe seasonal changes in zooplankton distributions, the association of these biological patterns with physical characteristics, and diel migrations of zooplankton (Flagg and Smith, 1989a; Smith et al., 1989, 1992; Plueddemann and Pinkel, 1989; Heywood et al., 1991; Roe and Griffiths, 1993; Ashjian et al., 1994; Flagg et al., 1994a, b; Heywood, 1996). Like other acoustic or optical (e.g. optical plankton counter) instruments, the species or size composition of the particles producing the backscatter signal detected by the ADCP cannot be identified absolutely (e.g. Smith et al., 1992). However, for the ADCP, significant correlations have been observed between backscatter intensity and mesozooplankton biomass, suggesting that a relationship between the abundance of mesozooplankton, or larger organisms present in constant proportion to mesozooplankton biomass (e.g. Sheldon et al., 1972), and the backscatter intensity does exist. Furthermore, the patterns described from the backscatter intensity are consistent with patterns observed in the mesozooplankton using conventional sampling techniques (e.g. Ashjian et al., 1994; Lyons et al., 1994; Buchholz et al., 1995; Heywood, 1996).

An excellent opportunity to study seasonal changes in vertical migration behavior of the zooplankton community over the continental shelf of the western North Atlantic Ocean was presented during SEEP-II (Shelf-Edge Exchange Processes in the Southern Middle Atlantic Bight) when a bottom-moored acoustic Doppler current profiler was deployed near the shelf break off the northeastern coast of the United States for 15 months (Flagg et al., 1994a). Seasonal changes in zooplankton biomass estimated with this instrument have been described (Flagg et al. 1994a). The ADCP used in this study was a four beam, single frequency (307 kHz) sonar transceiver which records, among other things, backscatter intensity from the transducer. The sensitivity of the sonar to the particles of interest (zooplankton) is inversely proportional to a characteristic size raised to the fourth power. Only when the particles are considered in aggregate do they yield a sufficiently large acoustic return to be detected. In practice, good correlations between acoustic backscatter intensity and zooplankton biomass estimates from 1 m<sup>2</sup> MOCNESS (Wiebe et al., 1976) equipped with 149  $\mu$ m mesh nets have been found (e.g. Flagg and Smith, 1989 a and b; Heywood et al., 1991; Ashjian et al., 1994; Flagg et al., 1994a, b). In principal, there is a dependence on the acoustic impedance (mostly size) distribution of the particles although, as yet, an impact of variations in size class distribution in data collected in widely separated regions has not been discerned.

For the study at hand, the ADCP offers significant advantage over conventional sampling with nets. The greatest advantage is that the ADCP profiles the water column about once per second which samples the temporally varying zooplankton field with greater temporal and vertical resolution than otherwise possible. Moored ADCPs also may be deployed on station continuously for many months making it possible to examine seasonal as well as meso-scale and diurnal variations. Many of the patterns described using acoustically derived estimates of biomass are consistent with those expected or described based on information from net sampling. Because intensity varies on a logarithmic scale rather than a linear scale, backscatter intensity data are routinely converted to estimated equivalent zooplankton biomass (e.g. Heywood et al., 1991; Ashjian et al., 1994; Flagg et al., 1994a, b). Acoustic data may not be robust

for measuring absolute biomass of zooplankton but do permit the investigator to describe variations in the spatial and temporal distribution of biomass, vertical migration patterns, the seasonality and/or regional occurrence of migration within a data set, and the associations of such distributions or behaviors with physical features such as currents or water types at much greater resolution and over much greater areas and temporal periods than were possible using conventional net-based sampling.

The purpose of the present study was to address explicitly diel vertical migration of the zooplankton community at that site through a re-analysis of the data presented in Flagg et al. (1994a). The goals of the analysis were: (1) develop methods to identify quantitatively those periods during which diel vertical migration was occurring, (2) describe the biological and physical changes associated with inception or cessation of migration and assess the role of physical–biological interactions, (3) describe the migration pattern and compare vertical distributions during periods of migration and non-migration, and (4) identify environmental cues which may be associated with the timing of migration and/or changes in the migration amplitude.

## 2. Methods

### 2.1. Data collection

Data were collected during the SEEP-II program from mid-February, 1988, through mid-May, 1989. A 307 kHz acoustic Doppler current profiler was moored on the bottom at the edge of the continental shelf in the Shelf Water/Slope Water frontal zone at 37° 41.98' N and 74° 20.34' W. The instrument observed the 90 m water column for approximately 15 months. Acoustic backscatter intensity and velocity data were collected over three time periods: 17 February–7 June, 1988 (S2A), 28 June–19 October, 1988 (S2B), and 20 November 1988–2 May 1989 (S2C). Additional data collected at the mooring site during the deployment periods were chlorophyll *a* fluorescence at three depths (Medeiros and Wirick, 1992; Wirick, 1994;), near-surface radiation (C. Wirick, pers. comm.), and temperature at 13–16 depths. Wind data were obtained from a NOAA buoy off Delaware Bay (44009) and a C-Marr stationed at Chesapeake Bay (CHLV2) (National Buoy Data Center).

We present and discuss the acoustic backscatter intensity as estimated equivalent biomass. The 'estimated biomass' discussed in this paper was derived by a conversion of acoustic backscatter intensity to estimated biomass. Conversion of the acoustic backscatter intensity to estimated biomass was accomplished using methods described in Flagg and Smith (1989a, b) and is described for these data in Flagg et al. (1994a). Briefly, net tows were conducted in the vicinity of the mooring on four cruises in 1988. Samples were collected using the MOCNESS plankton net system (149  $\mu$ m mesh, 1 m<sup>2</sup> mouth area, Wiebe et al., 1976) on 17 February 1988, and on 29 June 1988, from the *R/V Endeavor* and with Bongo nets (153  $\mu$ m mesh) on 11 March 1988, and 9 June 1988, from the *R/V Cape Hatteras* and from the *R/V Endeavor*, respectively. All abundances were converted to dry weights and integrated water column biomass was

calculated (Lane et al., 1991). The relationship between zooplankton biomass at a particular depth and time and contemporaneous and spatially coincident backscatter intensity from the ADCP was established using linear regression (see Flagg et al., 1994a). All acoustic intensities were converted to estimated equivalent zooplankton biomass according to the equation in Flagg et al. (1994a).

## 2.2. Acoustically derived/estimated biomass data

The acoustic backscatter intensity data were reduced to hourly averages of estimated equivalent zooplankton biomass in fifteen, 5 m depth bins ranging from 10 to 85 m. The depth below which 50% of the estimated biomass in the water column was located (integrated from the bottom to the top) was calculated for each hour. This statistic, referred to hereafter as the median depth of the water column estimated biomass, was then used to explore diel vertical migration patterns. For most of the analyses, the time series of the median depth was band-pass filtered with half-power cut off at 6 and 40 h to isolate the signal both from high frequency internal wave induced fluctuations and meso-scale variations.

## 2.3. Identification of migration periods

The identification of periods of significant vertical migration and the description of the typical diel pattern of the depth distribution of estimated equivalent zooplankton biomass during this migration were accomplished simultaneously. A method of identifying days and periods of DVM was sought that would be a useful description for all data sets, regardless of the vertical distribution of estimated biomass or the duration of migration periods. We selected a criterion for DVM which was based on the rate of change of the median depth of the estimated biomass throughout the day. In selecting an optimal method for quantitative identification of periods of diel vertical migration (DVM), we worked extensively with the first segment of the data set (S2A) which contained both vigorous and weak periods of migration. We wished to consider the diel pattern in the vertical distribution without regard to daily changes in the amplitude of migration, represented here as the range over which the median depth of the biomass varied, or changes in the length of the daylight period throughout the year. Therefore, time of day was normalized so that sunrise and sunset always occurred at 0600 and 1800. Thus, if the interval between the actual sunset and sunrise was less than 12 h, the night time clock was sped up proportionately, and *vice versa* for nights when the interval was more than 12 h. A similar adjustment was made to the day time clock so that the normalized daylight period also was 12 h and the day length remained at 24 h. The period of daylight then was 12 h throughout the data set, allowing direct comparison of the timing of migrations between winter and summer periods which are characterized by distinctly different light periods. It also facilitated the use of sinusoids to describe the vertical displacement of biomass. This standardization of course precludes investigation of day-length specific effects in the data.

The median, estimated biomass depths also were normalized relative to the maximum and minimum depth observed within each 24 h period, with the day beginning

at 0000 h and ending at 2300 h (local standardized time). The minimum depth was assigned a value of 0 and the maximum depth a value of 1.0, with other values ranging from 0 to 1.0. The normalization of the median depths emphasizes the timing of changes in distribution rather than the actual daily migration ranges. Since the ADCP cannot 'see' the upper 10 m of the water column (Flagg and Smith, 1989a), consideration of actual median depths should be conducted with care because significant biomass may be out of range; this does not diminish the utility of the instrument for examining changes in the vertical distribution of biomass especially when considering depth-normalized data.

For a zooplankton community undergoing DVM, the greatest downward velocity should occur near sunrise (0600) and the greatest upward vertical velocity near sunset (1800). The vertical migration velocity pattern through a 24 h period of a community undergoing DVM can be approximated roughly by a sine curve. For each day, hourly 'vertical velocities' ( $v_i$ ) were calculated using the depth-normalized, time-standardized median biomass depths. A 24 h sinusoid was fitted, in a least-squares sense, to the vertical velocities for each day:

$$\hat{v}_i = a \sin(2\pi t_i/24) \quad (1)$$

where  $t_i$  is the standardized time and

$$a = \sum_{i=1}^{24} (v_i \sin(2\pi t_i/24)) / \sum_{i=1}^{24} \sin^2(2\pi t_i/24) \quad (2)$$

The 'goodness of fit' to the idealized curve was assessed by calculating a normalized error term defined as the ratio between the mean square error of the fit and the square of the derived amplitude,  $a$ :

$$\text{Normalized mean square error} = E^2/a^2 \quad (3)$$

where

$$E^2 = \sum_{i=1}^{24} (v_i - \hat{v}_i)^2 \quad (4)$$

The statistical significance of the fit for each day was determined using randomization testing (e.g. Manly, 1991). This involves the generation of a series of  $n$  randomized daily velocity series composed of velocities determined for a particular day which had been re-ordered in random order and the calculation of the goodness of fit of each of the randomized curves to the predicted sinusoid. The probability ( $\hat{p}$ ) that the least-squares fit of the actual data was not a random event was calculated by

$$\hat{p} = \frac{\# \text{ random curves with smaller error than observed curve}}{\text{total } \# \text{ of randomizations } (n)} \quad (5)$$

with the standard error of  $\hat{p}$  defined by

$$\text{Standard Error of } \hat{p} = \sqrt{(\hat{p}(1 - \hat{p})/n)} \quad (6)$$

In order to obtain standard errors of order of magnitude of 0.001, 10,000 random curves were generated for each day in the data. For 24 random numbers, there are approximately  $6.2 \times 10^{23}$  possible orderings of 24 numbers which greatly exceeds 10,000. The sequences of vertical velocities generated by the randomizations were checked to insure that changes in velocity between adjacent values did not exceed the maximum change observed in the actual data. The analysis was done separately for each of the three segments of the SEEP II data set (S2A, S2B, and S2C).

The least-squares fit of vertical velocity was a satisfactory method to identify periods of DVM because it focused on the actual vertical displacement of the estimated biomass, the key characteristic of DVM. Thus, this model is a robust description of diel vertical migration.

### 3. Results

#### 3.1. General features of the zooplankton biomass and environment

Seasonal changes in total estimated biomass for the three data sets have been described by Flagg et al. (1994a). Integrated, estimated biomass for the water column for each day of the three segments is presented here to place the migration analysis in context (Fig. 1). Generally, estimated biomass increased throughout the spring, with greatest levels observed in late spring (S2A: May 1988 and S2C: April 1989). Estimated biomass decreased during the formation of seasonal thermal stratification in May and remained relatively low throughout summer (S2B), fall, and winter (S2C), with some increases during late summer 1988 (August) and spring of 1989 (March–April). The brief spikes in the data likely resulted from advective events. The median depth of the estimated biomass (not shown) was between 40 and 50 m during spring and fall and between 30 and 40 m during summer.

The physical characteristics of the water column varied seasonally (Flagg et al., 1994a) with the winter and early spring being characterized by a well-mixed water column (Fig. 1). A strong thermocline developed in late May and persisted throughout the summer until late fall, when the water column again became well-mixed. Along-shore winds were strongly correlated with alongshore currents, although the expected  $\sim 12$  h lag between wind and currents is not resolved by this method (Table 1). The stratification of the water column during late spring was periodically disrupted by wind-induced advective events (e.g. 30 April 1988 and 4 May 1988), when southwesterly alongshore winds produced onshore movement of the shelf/slope front at the surface and offshore movement near the bottom. As a result, southwest currents were correlated with decreased stratification.

Chlorophyll *a* concentrations, integrated over the water column and near the surface, followed the seasonal progression expected for the temperate zone, with greatest concentrations in spring and lowest concentrations in summer (Fig. 1). Sporadic, abrupt enhancement or diminishment of chlorophyll *a* concentrations were associated with advective events which transported water masses of differing characteristics over the mooring site (see especially 10–20 May 1988) (Fig. 1, Table 1) (Flagg et al., 1994a).

### 3.2. Characteristics of estimated biomass distributions

Vertical distributions of estimated biomass and the median depth from two separate weeks during the first (S2A) deployment illustrate periods when DVM was occurring (3–9 March 1988) and also when the migration signal was absent (20–26 April 1988) (Figs. 2 and 3). Normalization and standardization of the median depth preserved the patterns in the vertical distribution of the biomass (Fig. 2), while allowing direct comparison of days with different light and dark periods and migration amplitudes. The week of 3–9 March was characterized by strong diel vertical migration, as demonstrated by the normalized mean depth of estimated biomass (Fig. 2a; upper panel). The times of upward and downward migration clearly were synchronized with the times of sunset and sunrise (Fig. 2a; lower panel). Note that the actual depth distribution exhibited considerable variability about a sinusoidal curve. The week of 20–26 April exhibited a highly irregular distribution of estimated biomass with little discernible diel migration pattern (Fig. 2b; upper panel). The vertical velocities of estimated biomass for this week showed little synchronization of the upward or downward movement of estimated biomass with the times of sunset or sunrise (Fig. 2b; lower panel).

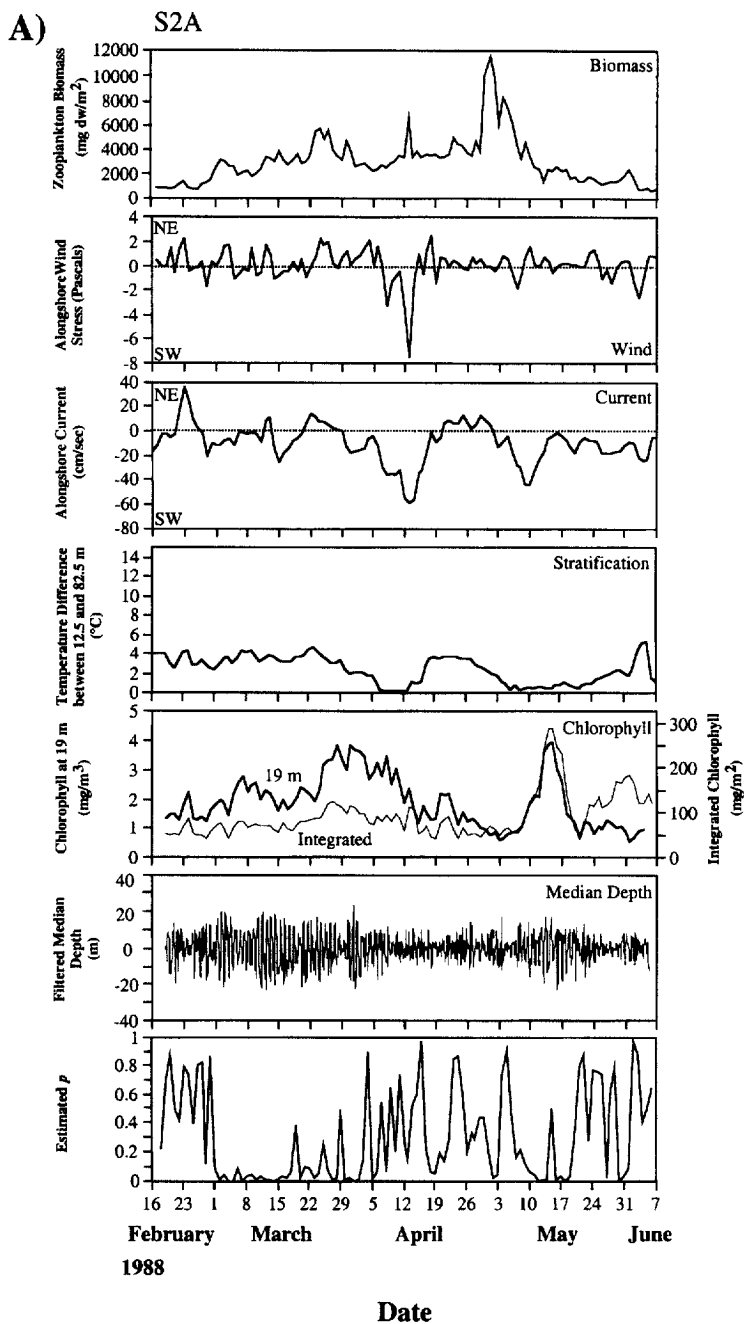
Average vertical distributions of estimated biomass for 4 h periods centered on noon and midnight for the same two weeks demonstrated a marked change in the day/night distributions when DVM was present in March, while there was little day/night difference in the general vertical distribution for the week in April (Fig. 3). Low variability in the mean distribution of estimated biomass was observed in the mean distribution during the diel vertical migration period (3–9 March) when a distinct and fairly narrow estimated biomass maximum was observed at depth during the day, possibly constrained by the sea floor. In contrast, considerable variability was observed when estimated biomass was high in the upper water column, both at night during the week during which DVM occurred (3–9 March) and for day and night when migration was absent (20–26 April) (Fig. 3). This upper-water column variability may have resulted from patchiness in the biomass at the mooring site, from individuals moving in and out of the upper layer of the water column at night, or from the inability of the upward looking ADCP to profile the upper 8.2 m of the water column (Flagg et al., 1994a).

### 3.3. Occurrence of a diel vertical migration pattern in the SEEP data sets

The daily estimated  $p$  values (Eq. (5)) which indicate the probability that the observed velocity curve follows a sinusoid, from the three deployments demonstrated

Fig. 1. Mean integrated water column estimated biomass ( $\text{mg dry weight m}^{-2}$ ), environmental characteristics (daily averages), filtered median depth of the zooplankton biomass (band-pass filtered between 6 and 40 h), and the probability that the observed daily vertical distribution of biomass was consistent with diel vertical migration (estimated  $p$ ) for the (a) spring (S2A), (b) summer (S2B), and (c) fall/winter (S2C) deployments. Integrated water column chlorophyll  $a$  estimated from through interpolation based on a regression between temperature as measured by thermistors and fluorescence from fluorometers at three depths and integrated from surface to bottom (Wirick, 1994).





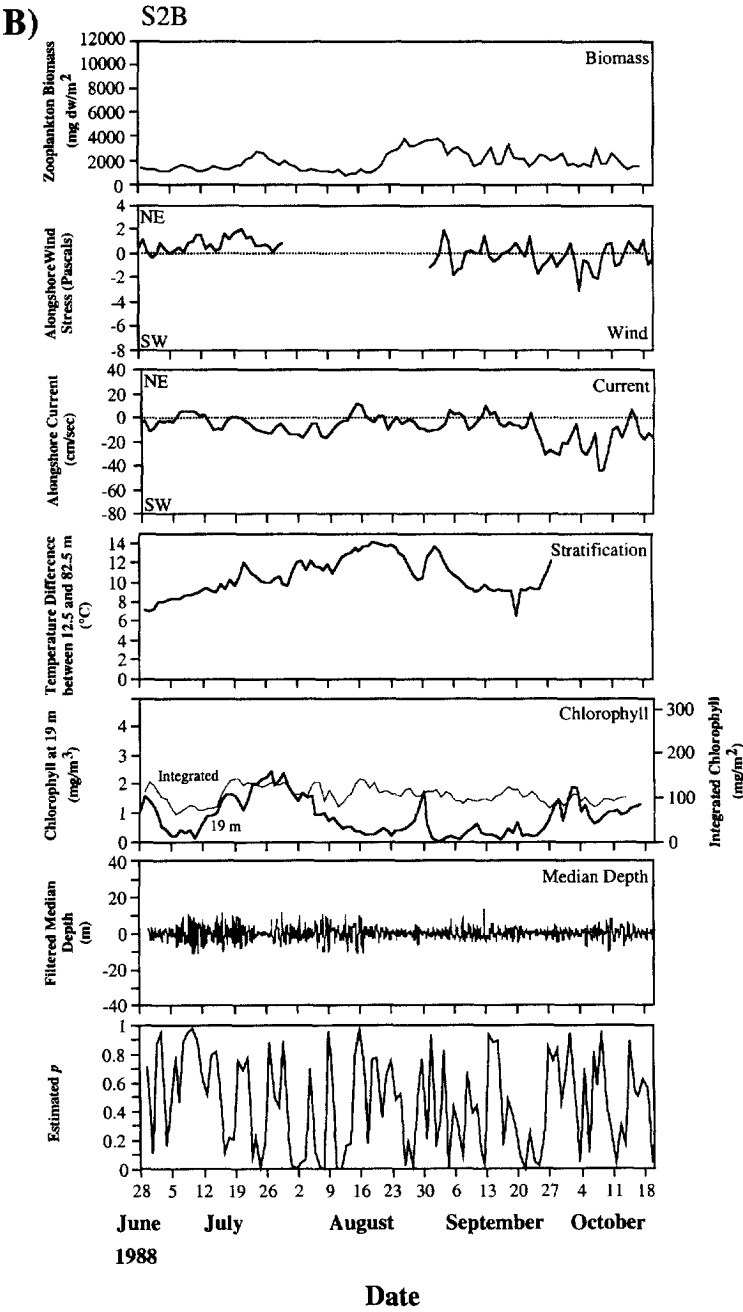


Fig. 1. (Continued.)

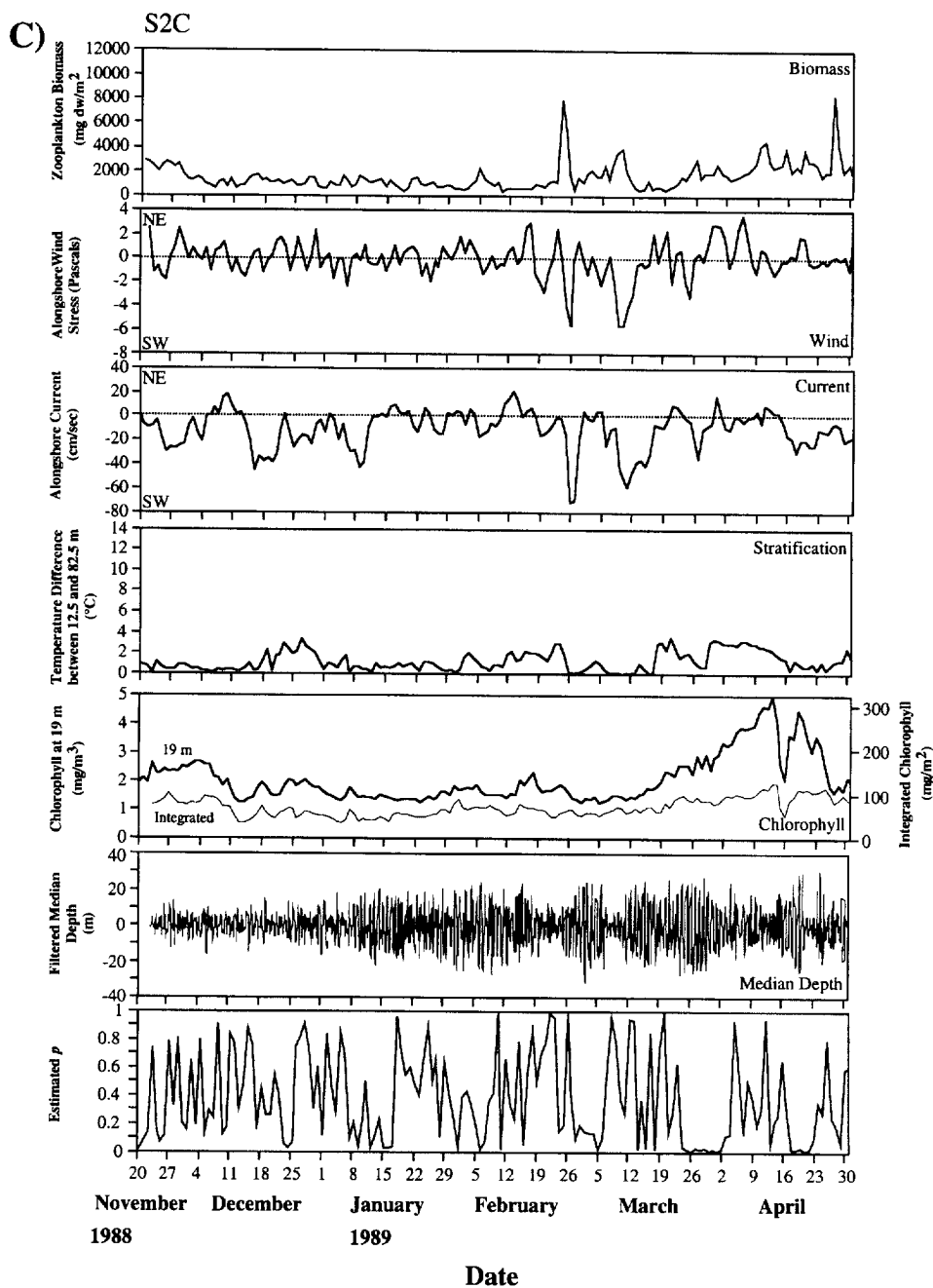


Fig. 1. (Continued.)

Table 1

Correlation coefficients between environmental variables (daily averages) and estimated  $p$  for the least-squares fit of observed hourly vertical velocities of estimated biomass to an ideal, sinusoidal distribution under DVM for each day for the three data sets. Only coefficients significant at the 0.05 level or greater are listed. Coefficients significant at the 0.001 level are noted with the \*\*. Coefficients were calculated with up to five days lag between the data sets; only the greatest values are shown. Lag, in days, is noted for each significant comparison. In this table, a negative lag indicates that the variable in the column is lagged relative to the variable in the row

|                        | Alongshore Current<br>(cm s <sup>-1</sup> ) | Alongshore Wind Stress<br>(Pa) | Temperature Difference<br>(°C) | Chlorophyll at 19 m<br>(mg m <sup>-3</sup> ) | Integrated Chlorophyll<br>(mg m <sup>-2</sup> ) | Estimated $p$ |
|------------------------|---|--------------------------------|--------------------------------|--|---|---------------|
| S2A                    |   |                                |                                |  |   |               |
| Alongshore current     | 0.498**                                     |                                |                                |  |   |               |
| Alongshore wind stress | 0.653**(-3)                                 | 0.262(-1)                      |                                |  |   |               |
| Temperature difference | -   | 0.195(+3)                      | -0.149(+5)                     |  |   |               |
| Chlorophyll at 19 m    | -0.351**(+5)                                | -                              | -0.410**(+5)                   | 0.362**                                      |   |               |
| Integrated chlorophyll | -   | -0.154(-4)                     | -                              | -0.394**(-5)                                 | -0.167(-2)                                      |               |
| Estimated $p$          | 113   | 112                            | 112                            | 107  | 108   | 110           |
| S2B                    |   |                                |                                |  |   |               |
| Alongshore current     | 0.452**                                     |                                |                                |  |   |               |
| Alongshore wind stress | -   | -0.235(-5)                     |                                |  |   |               |
| Temperature difference | -0.343**(+1)                                | 0.255(+1)                      | 0.350                          | 0.400**                                      |   |               |
| Chlorophyll at 19 m    | -   | 0.326                          | -                              | -  | -0.242  |               |
| Integrated chlorophyll | -   | -                              | 92                             | 112  | 108   | 113           |
| Estimated $p$          | 115   | 83                             |                                |  |   |               |
| S2C                    |   |                                |                                |  |   |               |
| Alongshore current     | 0.491**(-1)                                 |                                |                                |  |   |               |
| Alongshore wind stress | 0.279**                                     | 0.391**(+1)                    |                                |  |   |               |
| Temperature difference | -   | 0.289**(+1)                    | 0.441**(+1)                    |  |   |               |
| Chlorophyll at 19 m    | 0.188(-4)                                   | 0.239(+2)                      | 0.332**(+2)                    | 0.836**                                      |   |               |
| Integrated chlorophyll | 0.208(+5)                                   | -                              | -                              | -0.192                                       | -0.211  |               |
| Estimated $p$          | 172   | 163                            | 167                            | 171  | 162   | 163           |

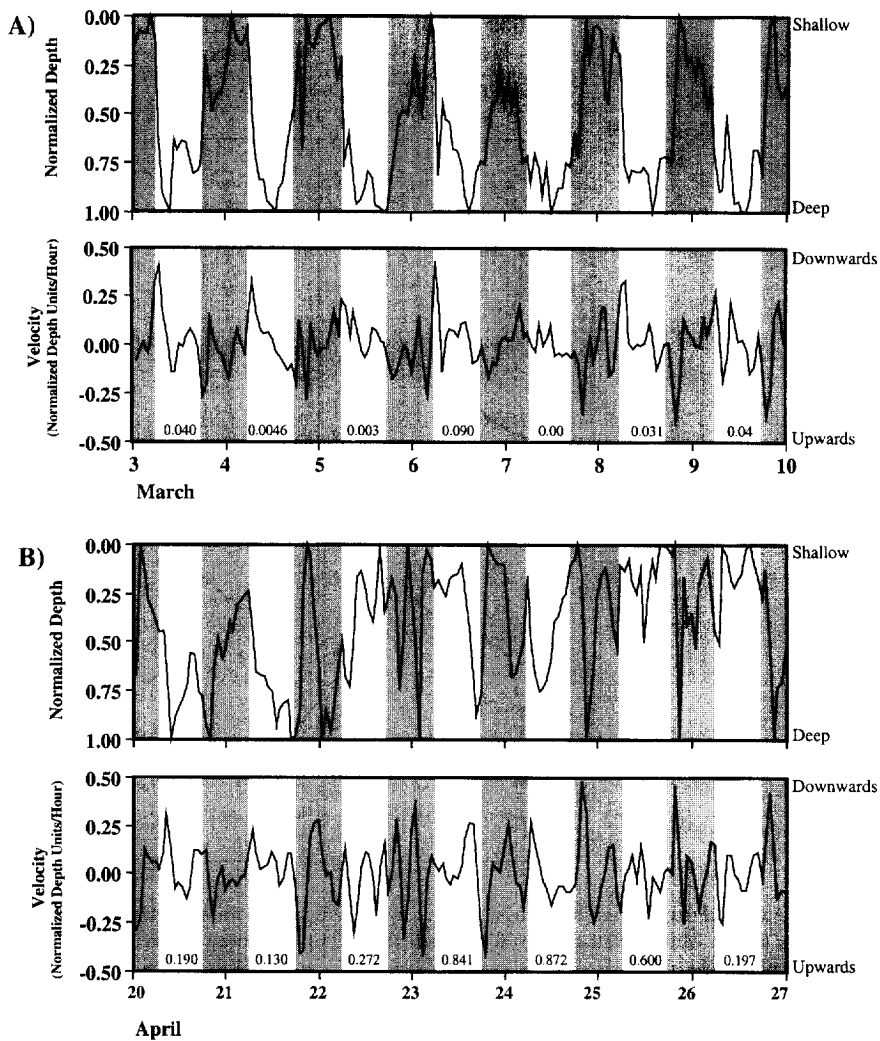


Fig. 2. Median depth of the estimated biomass (upper panel), normalized relative to maximum and minimum depths for each day, hourly vertical velocities of the estimated biomass (lower panel), and timing of day and night (shaded sections represent periods of night) for (a) 3–8 March 1988 and (b) 20–26 April 1988. The probability that the observed daily vertical distribution of biomass was consistent with diel vertical migration (estimated  $p$ ) is indicated for each day along horizontal axis of lower panel.

that the 'classic' diel vertical migration pattern (e.g. Cushing, 1951; Pearre, 1979; Forward, 1988) was present for 35, 17, and 20% ( $\hat{p} < 0.05$ ) of the days in the spring (S2A), summer (S2B), and fall/winter (S2C) deployments, respectively (Table 2; Fig. 1). This in turn indicated that diel vertical migration was *not* present for significant portions of the data records (65, 83, and 80% during spring (S2A), summer (S2B), and fall/winter (S2C), respectively, Table 2). The spring deployment documented the

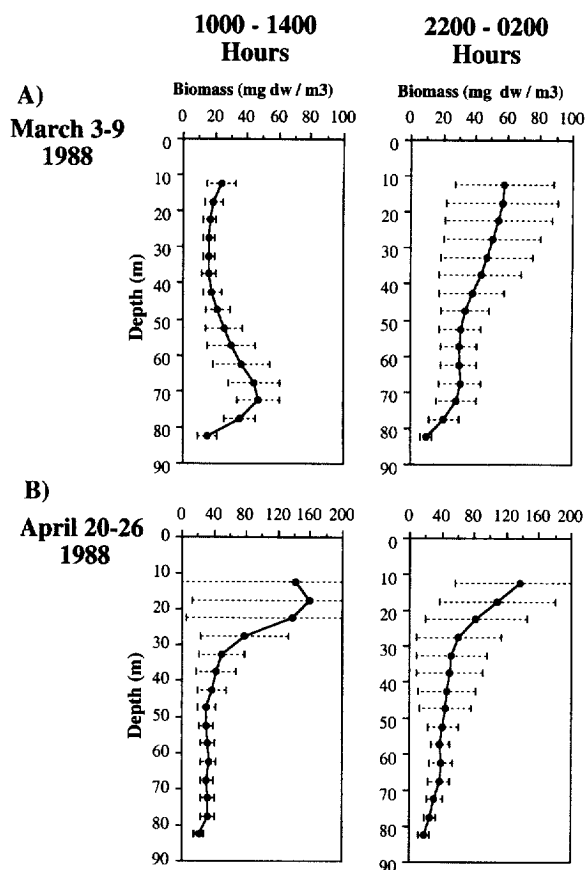


Fig. 3. Average vertical distribution of biomass for four hours centered on noon (1000–1400) and midnight (2200–0200) for (a) 3–8 March 1988 and (b) 20–26 April 1988. Error bars indicate one standard deviation. For each data point,  $N = 5$ .

longest period of continuous diel vertical migration ( $\sim 1$  March–3 April 1988 excepting a few days), with a shorter period occurring during most of the first 10 days in May (Fig. 1a). There were other isolated days or multi-day segments when the pattern was present (Fig. 1a); however, these two periods were the only extended periods of diel vertical migration in the 15-month record. No extended periods of migration occurred during the summer deployment (Fig. 1b). During the third (fall/winter) deployment, diel vertical migration was observed early in the spring bloom of 1989, 26 March–3 April (Fig. 1c; Flagg et al., 1994a). Isolated episodes of diel vertical migration occurred in the 1989 data record; however, in general, in the months for which there are data for both years the occurrence of the diel vertical was much reduced in 1989 compared to 1988.

Estimated biomass, after reaching the surface, was found at slightly deeper depths in the water column later during the night, often re-concentrating at shallower depths

Table 2

Statistics on the identification of periods of diel vertical migration by the vertical velocity method

| Data segment | Number of days in segment (n) | Proportion (number) of days with |            |
|--------------|-------------------------------|----------------------------------|------------|
|              |                               | $p < 0.05$                       | $p < 0.10$ |
| S2A          | 110                           | 0.35 (38)                        | 0.46 (50)  |
| S2B          | 114                           | 0.15 (17)                        | 0.20 (23)  |
| S2C          | 163                           | 0.20 (32)                        | 0.28 (45)  |

immediately prior to the downward migration. This vertical distribution feature has been described as 'midnight sinking' (Russell, 1927; Raymont, 1963). Of the 38 days identified as being characterized by diel vertical migration during the spring deployment (S2A), 31 days (82%) were characterized by a midnight deepening of the estimated biomass, although the deepening did not always occur at the same hour on each day.

Our analyses also demonstrated the difficulties of using reductive statistics that represent biomass distribution (i.e. median depth of estimated biomass) alone for identification of periods of DVM. The actual daily migration range of the estimated biomass (Fig. 1) frequently appeared to be large ( $\pm 20$  m), especially during the spring (S2A) and fall/winter (S2C) deployments, suggesting that extended periods of large amplitude daily migrations had occurred. However, comparison with estimated  $\hat{p}$  indicated that the periods of diel vertical migration were considerably less extensive than large migration ranges suggested. Closer examination of the data on migration range revealed that, although the amplitude of the daily range of estimated biomass median depth was large, sustained, and apparently regular (Fig. 1) for periods of several weeks, the actual timing of the vertical redistribution of median estimated biomass was not regular with respect to the timing of sunrise and sunset. This suggests that statistics based only on the total depth range of estimated biomass, for example, without consideration of the timing of changes in the depth distribution of estimated biomass, could be misleading, and could encourage an investigator to conclude erroneously that diel vertical migration is present. Two components of DVM, amplitude and timing, must be measured simultaneously for DVM to be identified unambiguously.

### 3.4. Factors influencing the occurrence of DVM: External environmental effects

Daily averages of selected environmental variables (alongshore wind stress, alongshore current at 22.5 m, temperature differential between 12.5 and 87.5 m (indicative of stratification), chlorophyll *a* at 19 m, vertically integrated chlorophyll *a*) were compared to the daily  $\hat{p}$  values (Fig. 1, Table 1) to establish relationships between the presence of diel vertical migration and characteristics of the environment. (Note: Across-shelf currents and winds, although measured, were found to be less important

to patterns in estimated biomass distributions than alongshore currents and winds in the previous analysis of these data (Flagg et al., 1994a)).

Episodic changes in the environment were associated with the presence or absence of migration over the mooring, probably because of the introduction of different populations and water types as a consequence of advection. Wind-induced current fluctuations had the most influence on both the physical and biological regimes (see also Flagg et al., 1994a). These influences were especially evident during the spring (S2A) deployment. The extended period of diel vertical migration during March 1988 occurred during the spring bloom when elevated concentrations of chlorophyll *a* at 19 m, and throughout the water column, were observed and stratification was weak. From 6 to 13 April, strong alongshore winds produced southwesterly alongshore currents and eliminated the stratification of the water column through a combination of vertical mixing and sheared cross-isobath flow. Chlorophyll *a* concentrations at 19 m declined by approximately 50% during the advective event. The cessation of diel vertical migration of the acoustically estimated biomass that occurred at the beginning of April was associated with the commencement of this strong advective event. Alongshore currents diminished following the wind event, with subsequent re-establishment of a stratified water column. Diel vertical migration, however, was not re-established and chlorophyll *a* concentrations at 19 m remained low.

Subsequently, another strong advective event began on approximately May 10 and also was associated with a breakdown of water column stratification. During this event, water with high chlorophyll *a* concentrations and a resident population of vertically migrating species (DVM present) was advected over the mooring site (Fig. 1). Following relaxation of the wind on 11 May, stratification of the water column was re-established over the mooring, accompanied by a gradual cessation of the pattern of diel vertical migration of the acoustically estimated biomass and a dramatic reduction in chlorophyll *a* levels (75%).

Although periods of diel vertical migration were not as prolonged during the spring 1989 (S2C deployment) as during spring 1988 (S2A), the inception and cessation of diel vertical migration in the acoustically estimated biomass was associated at some times with wind and advective events. For example, some diel vertical migration associated with strong southwesterly alongshore flow was observed in mid-January 1989 (Fig. 1). Another diel vertical migration event, 28 February–6 March 1989, began following very strong southwesterly flow and ended during a subsequent advective event, also toward the southwest. The diel migration periods of 24 March–3 April 1989, and 17–24 April 1989, likewise were associated with strong southwesterly flow elements. Wind events also were associated with changes in the currents and water column stratification during the summer of 1988 (S2B deployment), although wind stress magnitudes were less during the summer months. Hence, advection apparently transported different water types, and their intrinsic plankton communities, over the mooring site.

On a daily basis, however, correlations among the physical variables (winds, currents, temperature, and stratification) and the presence of diel vertical migration were poor (Table 1). The occurrence of the diel vertical migration pattern was negatively, and weakly, correlated with chlorophyll *a* concentrations (both integrated



over the water column and at 19 m) for all three segments (Table 1). These observations indicate that the presence of diel vertical migration in the zooplankton population at the mooring site on the shelf was influenced primarily by the advection of water containing vertically migrating taxa over the site, either from the Slope Water to the east or from regions to the north of the Middle Atlantic Bight. The reduction of vertical migration during the summer months coincides both with ontogenetic cessation of migration by the vertically migrating taxa (e.g. *Calanus finmarchicus*) and reduced intensity of wind stress and advection at the site. The decreased advection then would reduce the possibility of episodic transport of non-local populations, with potentially different migration characteristics (e.g. vertically migrating), over the site. Both mechanisms, acting alone or in concert, potentially may affect the occurrence of migrating taxa on the shelf.

### 3.5. Factors influencing the occurrence of DVM: light as a cue for migration

The extended period of diel vertical migration that occurred in March 1988 during the spring (2A) deployment was used to explore the characteristics of temporal changes in the distribution of estimated biomass with depth during migration and to identify any synchronization of vertical migration with the light cycle. Hourly-averaged, estimated biomass observations within each 5 m depth interval were converted to proportions of the total estimated biomass occupying the entire water column for each hour. Averages and standard deviations then were computed for each depth for March 1988. The average hourly vertical distribution of estimated biomass

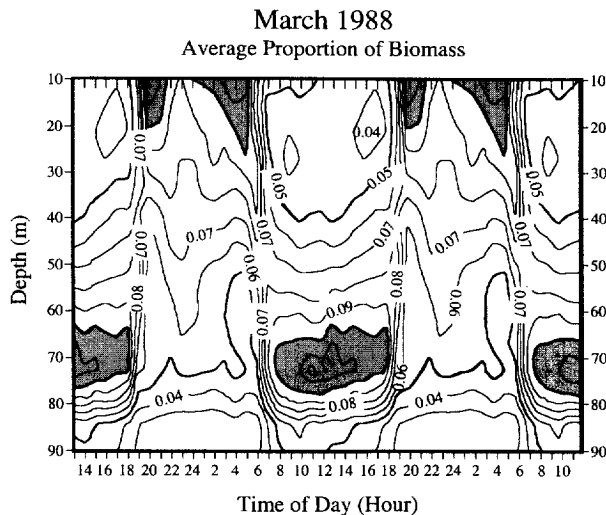


Fig. 4. Average biomass distribution, as proportion of the total biomass for the water column for each hour, with depth for March 1988. Times were standardized to sunrise (0600) and sunset (1800) prior to calculation of the averages. Shading indicates greater than 0.1 (10%) of the total water column biomass for that hour.

showed several previously described characteristics consistent with the classical pattern (Fig. 4). Greatest estimated biomass was found at depth during the day and near the surface at night. Migrations were accomplished cohesively, with much of the estimated biomass undergoing vertical displacement simultaneously at 0600 and 1800 h, the times of sunrise and sunset, respectively, in standardized time.

Hourly-averaged light intensities (C. Wirick, pers. comm.) and vertical velocities of estimated biomass were used to explore the synchronization of sunrise/sunset and vertical migration during the month of March 1988. Hourly averages over the month were calculated for both light and velocity (Fig. 5). Downward movement in the morning either preceded discernible light or was accomplished at the very low light levels existing at 0500 and 0600 h. The average light level at the inception of downward migration was  $0.78 \pm 3.80 \mu\text{E m}^{-2} \text{s}^{-1}$  (mean  $\pm$  S.D.), with an average light level of only  $2.77 \pm 8.81 \mu\text{E m}^{-2} \text{s}^{-1}$  at maximum downward migration velocity. Upward movement in the evening was initiated when measurable light was still present ( $\sim 1700$  h), at  $11.53 \pm 11.37 \mu\text{E m}^{-2} \text{s}^{-1}$  (mean  $\pm$  S.D.), and peak upward movement occurred at sunset (1800 h), when average light intensity was  $3.10 \pm 5.07 \mu\text{E m}^{-2} \text{s}^{-1}$ . No consistent relationships were observed between the rate of change of light intensity and the timing or occurrence of migration.

Differences between the times of peak upward and downward velocities and the occurrence of a light threshold of  $25 \mu\text{E m}^{-2} \text{s}^{-1}$  were calculated near sunset and sunrise, respectively, for each day in March 1988. This light threshold was selected because for most days it was reached or exceeded within the second hour of

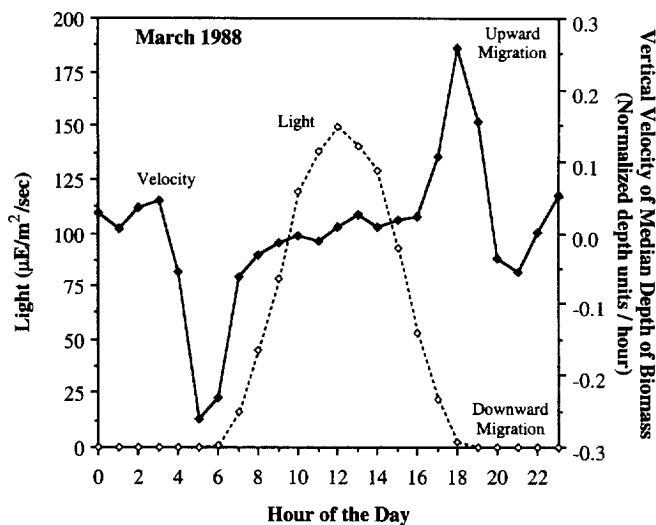


Fig. 5. Synchronization of periods of light and darkness with the peak upward and downward migration of zooplankton biomass for March 1988. Vertical velocity was calculated for each hour based on the depth normalized and time standardized data and then averaged by hour over the entire month. Light levels were time standardized and then the hourly averages were calculated. In this figure, downward migration is indicated by negative velocity values and upward migration is indicated by positive velocity values.

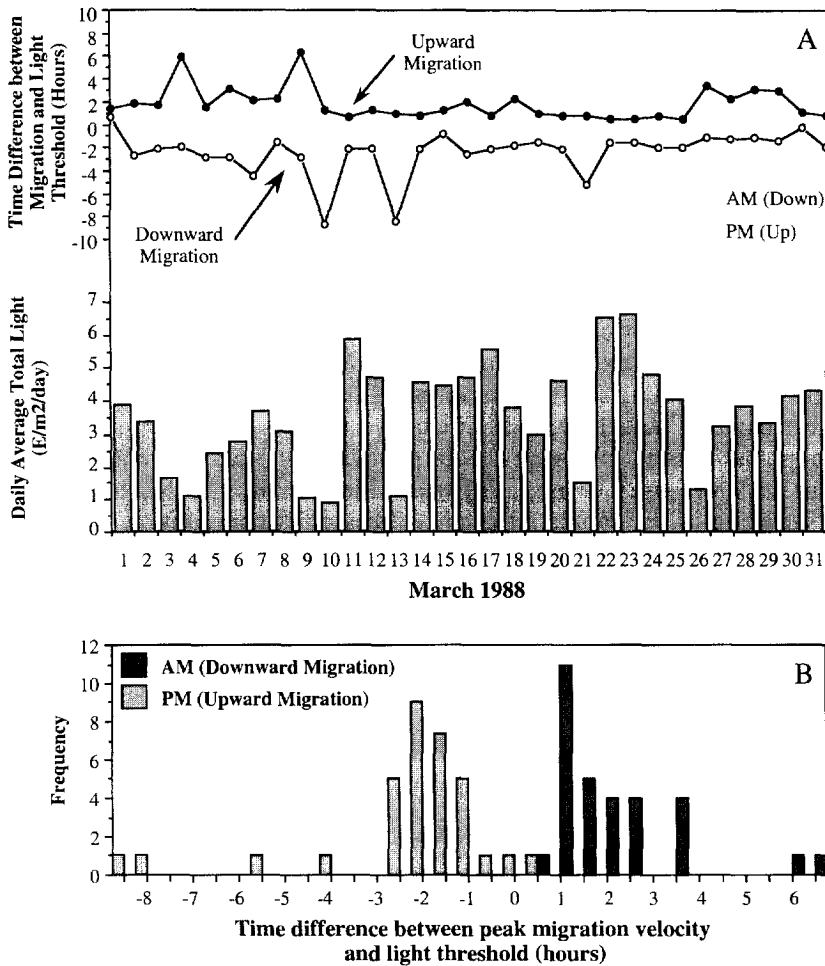


Fig. 6. (a) Comparison of time difference (hours) between occurrence of peak upward (PM) and downward (AM) vertical migration velocities and a light threshold of  $25 \mu\text{E m}^{-2} \text{s}^{-1}$  for March 1988 (upper curves) and the total light (integrated) at 19 m for each day (histograms). Time differences calculated from time standardized data. (b) Frequency distribution of time differences (h) between vertical migration velocities and a light threshold of  $25 \mu\text{E m}^{-2} \text{s}^{-1}$ .

measurable light. Most values were within 3 hours or less; however longer time differentials were calculated for days where measured light levels were especially low so that the threshold light level was reached later in the day (Fig. 6a). Generally, downward migration preceded the light threshold by 1.5–3 h, with a mode of 2.25–2.5 h (Fig. 6b). Upward migration was usually accomplished much nearer to the threshold, with the mode at 0.75–1.0 h. The distribution of time differences was broader for the downward movement than for the upward movement. The timing of diel vertical migration clearly is synchronized to the daily light cycle; however,

proximal cues (e.g. threshold intensity) for the inception of daily migration were not identified from our analyses.

### 3.6. Factors influencing the occurrence of DVM: species composition

Although ADCP backscatter intensity is not generated from the mesozooplankton alone (larger and air-containing plankton may contribute substantially to the signal), backscatter intensity has been shown to be correlated with mesozooplankton abundance over a large range of abundances. Significant correlations between mesozooplankton biomass and ADCP backscatter intensity have been observed in more than a few regions (Flagg and Smith, 1989a, b; Heywood et al., 1991; Ashjian et al., 1994; Flagg et al., 1994a, b), indicating that a relationship exists between intensity and mesozooplankton abundance. Despite the limitations of a single frequency acoustic transceiver and the technique used here, it is instructive to consider the composition of the mesozooplankton at the mooring site for periods when such information is available as an indication of whether migrating taxa were present.

Net sampling of the zooplankton provided species composition information for four times (two during the spring (S2A) and two at the start of the summer (S2B) deployments) (Lane et al., 1991). The combined, integrated, measured biomass of (1) adults and Copepodite Stage V and (2) Copepodite Stages I–IV of the vertically migrating species, *Calanus finmarchicus* and *Metridia lucens*, are shown relative to total measured biomass of the remaining zooplankton species, including non-migrating copepod genera (*Mesocalanus*, *Centropages*, *Pseudocalanus*) (Fig. 7) (e.g. Esterly, 1912; Bigelow, 1924; Clarke, 1933; Nicholls, 1933; Cushing, 1951). Total measured biomass of the migrating species was greatest on 11 March 1988, with ~50% of the

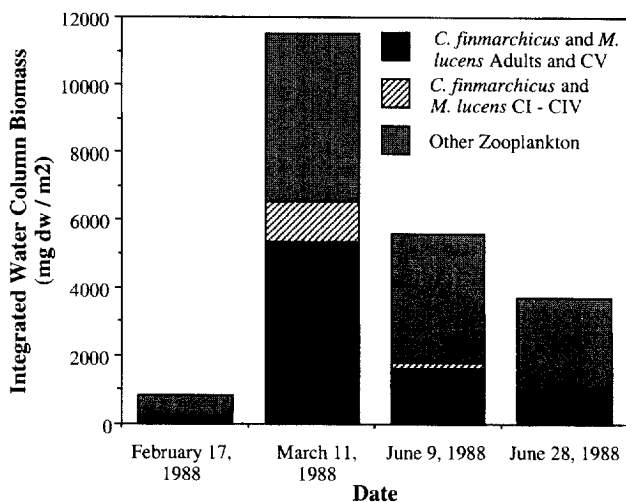


Fig. 7. Relative composition of the migrating vs non-migrating zooplankton species from the net tows conducted during the spring (S2A) deployment. Three or four tows were considered for each date.

total population being composed of migrating stages of the species *C. finmarchicus* and *M. lucens*. For the other three dates, these migrating species represented considerably less of the total measured biomass. Analysis of the ADCP estimated biomass record indicated that an extended period of diel vertical migration occurred during March 1988 (~1 March–3 April; Fig. 1). The strong migration signal observed in the acoustic data at that time may have been influenced in part from the large proportion of the zooplankton biomass composed of migrating species. *Calanus finmarchicus*, in particular, is large relative to the other species found in this region and should contribute significantly to the backscattered signal when it is present in abundance. The species composition, and presence of vertical migration on 11 March, contrasted markedly with the situation on 17 February 1988, where migration was not detected acoustically and vertically migrating species and life stages represented a small proportion of the total net-caught zooplankton biomass (~22%). Therefore, although the ADCP backscatter signal may result only in part from the mesozooplankton abundance, the diel vertical migration signal in the acoustic data during March was contemporaneous with the presence of mesozooplankton species for which diel vertical migration is a known characteristic.

#### 4. Discussion

Diel vertical migration was not a persistent characteristic of the zooplankton community at this site, at least as estimated from the acoustic backscatter intensity of the upward looking ADCP. The occurrence of vertical migration was associated primarily with the species composition and age-structure of the zooplankton and did not appear to be coupled to any local environmental characteristic of potential importance to zooplankton, such as food concentration, absolute light levels, or stratification of the water column. Rather, it appeared that the inception and cessation of migration at the site was driven by the advection to or from the site of populations or communities for which diel vertical migration was a characteristic strategy or behavior.

The diel vertical migration patterns observed in the acoustically derived biomass were consistent with the known life histories of the resident mesozooplankton. The most extended period of diel vertical migration detected in the backscatter intensity occurred in March 1988 (S2A). At this time, the mesozooplankton community was composed of significant proportions of late copepodite and adult stages of *Calanus finmarchicus* and *Metridia lucens*, both of which (species and life stage) may demonstrate diel vertical migration (community composition determined from net data). Hence, the diel vertical migration pattern evident in the backscatter intensity appears to give a fairly realistic picture of the migration of the mesozooplankton community. The cessation of migration in early April coincided with a strong advective event, which may have transported a different, non-migrating community over the site. The re-occurrence of migration in May followed a similar advective event during which a migrating community appeared to be re-introduced to the site. Possible sources of communities of migrating zooplankton include the Slope Water to

the east and the New York Bight region to the north (Grice and Hart, 1962; Judkins et al., 1980).

On a seasonal basis, the occurrence of migration may have been driven by succession in the zooplankton community and changes in the population age-structure over the shelf. For example, the onset of migration during March 1988 coincided with the time of maturation of the younger life stages of one of the dominant copepod species, *Calanus finmarchicus*. This species overwinters as a Copepodite Stage V with maturation and reproduction occurring in early spring (Marshall and Orr, 1955). The maturation during March of the first generation to the older life stages, for which DVM is a characteristic behavior, may have been associated with inception of DVM observed in the acoustic record at this time (e.g. Marshall and Orr, 1955; Pearre, 1979; Huntley and Brooks, 1982). The zooplankton samples collected during the study on 17 February 1988, (no DVM) and 11 March 1988, (strong DVM) support this hypothesis. On February 11, juveniles (copepodite stages I–IV) accounted for 43.4% of the total *C. finmarchicus* biomass, whereas on 11 March juveniles accounted for only 26.4% for the total *C. finmarchicus* biomass.

The dramatic change observed between the spring period, when the estimated biomass was experiencing episodic, prolonged periods of DVM, and the summer period, when the estimated biomass was not migrating, may be attributed to both seasonal changes in the zooplankton community composition and to ontogenetic changes in the migratory behavior of at least one of the species in the community. For example, species composition data from June 1988 at the mooring site indicated that mature stages of *Calanus finmarchicus* (C5 and adults) were present. However, these individuals were found at depth and were not migrating (data not shown). Seasonal or ontogenetic changes in the migration behavior of *C. finmarchicus* have been documented, indicating that later stages of the species move to depth during the warm summer months and do not migrate (Herman et al., 1981; Vidal in Falkowski, et al., 1983; Miller et al., 1991), and hence could not contribute to a diel signal in the distribution of estimated biomass.

Previous investigations of the zooplankton community over the continental shelf in New York Bight have demonstrated the seasonal changes in the community composition (Grice and Hart, 1962; Judkins et al., 1980). The most common copepod species in the winter-spring months were *Calanus finmarchicus*, *Metridia lucens*, *Pseudocalanus* sp., *Oithona similis*, and *Clausocalanus pergens*, of which both *C. finmarchicus* and *M. lucens* are considered vertical migrators, at least during these months (e.g. Esterly, 1912; Bigelow, 1924; Clarke, 1933; Nicholls, 1933; Cushing, 1951). In contrast, the copepod community in the summer was dominated by *Centropages typicus* and *Temora longicornis*, species not considered strong migrators. Preliminary analyses of zooplankton data collected over an 11 year period (1977–1987) during the MARMAP program from a  $1^\circ \times 1^\circ$  area around the mooring site demonstrated a similar seasonal succession in the community composition and population structure to those documented by Grice and Hart (1962) and Judkins et al. (1980) (Sherman, 1980, 1987; Green, pers. comm.). Hence, the gross seasonal changes in the distribution of estimated biomass at the mooring site were likely to have been a consequence of changes

in the zooplankton community composition, which in turn produced changes in the behavior of the zooplankton biomass.

Although clear statistical associations between DVM and environmental characteristics, such as chlorophyll *a* concentrations or water column temperature and stratification, were not detected, overall patterns regarding the occurrence of DVM and particular environmental conditions do emerge. DVM was associated with elevated levels of chlorophyll *a* in the water column, at least during the spring of 1988 (S2A deployment). Both periods of extended migration (March and May, 1988) in the data record occurred when elevated concentrations of chlorophyll *a* were observed. During periods when non-migrating populations were observed, concentrations of chlorophyll *a* were reduced and the zooplankton remained in the upper water column, where feeding could occur continuously over 24 h. These observations suggest that diel vertical migration may be advantageous only when sufficient food is available in the upper water column (e.g. Pearre, 1979). Food availability can influence both the occurrence of diel vertical migration and the migratory behavior of the population (e.g. Bohrer, 1980; Boyd et al., 1980; Huntley and Brooks, 1982; Dagg, 1985; Johnsen and Jakobsen, 1987; Conover et al., 1988). When food levels are reduced, the advantages of avoiding predation, for example, may be overshadowed by the necessity of obtaining sufficient energy (food) such that populations found in water types with reduced food conditions may not utilize DVM as a strategy (e.g. Johnsen and Jakobsen, 1987).

It has been suggested that DVM may occur when the environment, and the distribution of food, is stratified rather than being vertically homogeneous (e.g. Checkley et al., 1992). High concentrations of food are usually found in the euphotic zone in stratified systems, where susceptibility to visual predators is also increased. For our data set, however, DVM was not associated with periods of stratification; our most extended periods of DVM were observed when little stratification of the water column was present. A good example of this occurred in late April 1988, when stratification was re-established following a wind event but DVM, which had been present prior to the wind event, was not re-established. Additionally, DVM was next observed following a subsequent advective event (10 May) that transported a water mass characterized by DVM, elevated chlorophyll *a* levels, and a well mixed water column over the site. Observations from the summer of 1988 also contradict the suggestion of Checkley et al. (1992) since the water column was highly stratified during the summer, yet DVM did not occur. It is likely that, in our study, the zooplankton population during summer was composed of species for which DVM was not a strategy or of species for which the summer months are typically non-migratory due to ontogenetic changes in behavior.

Light frequently is considered to be a cue for the timing of diel vertical migration, since this environmental characteristic varies on a diel basis. The potential importance of light to migration is further emphasized by observations of Arctic zooplankton which do not undergo DVM during the continuous light of Arctic summer but return to this strategy once a more limited photoperiod has been re-established during autumn (e.g. Buchanan and Haney, 1980; Conover et al., 1988). Two hypotheses regarding the nature of the stimulus to the zooplankton have been advanced: The Preferendum Hypothesis and the Rate of Change Hypothesis (reviewed in Ringelberg,

1964; Forward, 1988). In the first, also referred to as the isolume hypothesis, the timing of migration corresponds to a particular light level or intensity such that the zooplankton follow the changing depth of a particular isolume. In the second, the rate and direction of change of light provides the cue or stimulus for the inception of migration. We attempted to identify one of these two hypotheses as the mechanism for the timing of migration in our data set.

The timing of evening upward migration was associated closely with the light cycle and the onset of darkness. Downward migration, however, usually preceded daylight and was accomplished during darkness. Several investigators have suggested that downward migration follows satiation and procurement of sufficient food (Pearre, 1979; Forward, 1988). Since different individuals may reach satiation at different times, downward migration should not be as coherent as upward migration. However, downward migration at dawn appeared to be fairly coherent in the present analysis.

Although the timing of migration corresponded with the diel light cycle, the nature of the stimulus was unclear from our analysis. Upward migration usually was initiated during low levels of light in the evening; however, there was no consistent association between a particular light intensity or isolume. Also there appeared to be little or no effect of the overall light intensity on the timing of upward migration on particular days since upward migration did not occur earlier on a cloudy day when light levels were reduced. In contrast, downward migration usually occurred in periods of darkness, before discernible light, suggesting that an endogenous rhythm may be influencing the timing of migration. Furthermore, we were unable to correlate the rate of change of light with the inception of vertical movement.

Evidence of a deepening of estimated biomass at midnight, or the 'midnight sinking' was observed for much of the migration period, occurring for 82% of the days during the March 1988 diel vertical migration period (e.g. Raymont, 1963; Hutchinson, 1967; Forward, 1988). It has been suggested that the apparent midnight sinking of biomass results when animals cease to maintain their position in the food-rich surface waters after satiation following their initial period of feeding (e.g. Conover, 1968; Rudjakov, 1970; Pearre, 1979; Simard et al., 1985). The subsequent rise in the water column may result from a renewed period of feeding prior to downward migration. The midnight sinking may potentially be a methodological artifact in some studies, since statistics reflecting the center of mass of biomass distributions in the water column may appear to deepen when a later "slug" of biomass migrates upward (see Pearre, 1979). In the present study, the mean estimated biomass distribution for the month of March (Fig. 4) indicated that migration was coherent and thus that the "midnight sinking" was not simply an artifact of the statistical reduction of data.

The moored acoustic Doppler current profiler was an effective and efficient instrument for resolving the temporal and spatial changes in the magnitude and distribution of backscatter intensity, and estimated biomass, at this location. The use of the ADCP to estimate biomass allowed us to examine the vertical migration pattern and the distribution of estimated biomass in the water column over many days and many depths and with considerably more temporal and spatial resolution than is possible from conventional (net) biomass methodologies. The contemporaneous collection of high resolution data on physical (temperature, currents, winds, light) and biological



(estimated biomass, chlorophyll *a* concentration) characteristics permitted a rigorous examination of the bio-physical interactions and seasonal associations at this site. This study demonstrated the value long (year) studies of biological and physical systems to our understanding of seasonal cycles in standing stocks, associations between physical and biological parameters, and temporal patterns and variations in the vertical distribution of these parameters. Furthermore, the study demonstrated the utility of moored instrumentation to the description of seasonal cycles in biological systems. From our analyses, it is clear that the occurrence of the diel vertical migration at the site was a function of multiple factors, both physical (e.g. advection, stratification, light) and biological (e.g. population specific life histories), that interacted to produce the observed patterns.

### Acknowledgements

The assistance of B. Behrens, T. Johnston, P. Lane, M. Sengco, E. Schwarting, and C. Wirick in the collection and reduction of the data is gratefully acknowledged. We are grateful to J. Green of the National Marine Fisheries Service for access to the MARMAP data, to J. Goulet for assistance with the data analysis, and to A. Solow for assistance in the statistical calculation of estimated *p*. Thanks to P. Lane and two anonymous reviewers for helpful comments which strengthened this manuscript. This research was supported by the U. S. Department of Energy under Contract No. DE-AC2-76CH00016, the Office of Naval Research under contract Nos. N00014-88-F-0097 and N0014-94-1-0361, and a Woods Hole Oceanographic Institution Postdoctoral Fellowship to C. J. Ashjian.

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